

CLATHRACEAE IN CALIFORNIA

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Although the Phallales are found mainly in tropical regions there are a few representatives known from temperate areas. Of the two families comprising this order of fungi, the Phallaceae are better represented in the north temperate zone than are the Clathraceae. Nevertheless, many collections have been reported in the United States of some members of the latter family.

The literature on those clathraceous fungi which have been collected in North America is very scattered. In eastern North America, Burt (1894) described *Anthurus borealis* from material collected in New England, and Murrill (1912) added a report, illustrated with a colored plate, of a collection of this species from Blackwell's Island, New York. It is possible that Burt's species and Murrill's record were based on imported material since it has been shown that *Anthurus borealis* Burt is a synonym of *Lysurus sulcatus* (Cooke & Masee) G. H. Cunningham, a species usually found in Australia. *Lysurus texensis* Ellis appeared as a *nomen nudum* in a casual collector's report (Gerard, 1880), and Long (1917) later published a description of another collection from Texas which he provisionally assigned to *L. texensis* Ellis. Lloyd's Synopsis (1909) has not been very useful for North American workers. It is a compilation in which several species are described briefly and illustrated, sometimes poorly; some of these descriptions may prove to represent the same taxon. In "The Genera of Fungi" by Clements and Shear (1931), both *Anthurus* and *Lysurus* are illustrated, the classic illustration of *Lysurus mokusin* credited to Cibot being copied there. Likewise, this illustration is used by Gäumann and Dodge (1928) but credited to "Cibot and Fischer" rather than to "Cibot in Fischer." Coker and Couch (1928) present a description of *Anthurus* and cite the above-mentioned illustrations.

The structure and development of the fruiting body of *Anthurus borealis* were described in considerable detail both by Burt in 1894 and by White in 1944. White referred the material that he studied to *Lysurus sulcatus*. A summary of these two studies was made by Rea and Heidenhain (1955) and a comparison of the characteristics of this species with those of *Lysurus mokusin* was made. This publication, based on the extensive observations made by Rea on specimens from Santa Barbara, California, of *Lysurus mokusin* (Cibot ex Pers.) Fries, represents the first detailed study of material collected in the western part of the United States.

Following his retirement from the directorship of the Santa Barbara Natural History Museum, Paul Marshall Rea devoted much time to

MADROÑO, Vol. 16, No. 2, pp. 33-76. April 18, 1961.

mycological studies in the Santa Barbara area. His collections and notes are deposited in the Herbarium of the University of Michigan, Ann Arbor, where, through the courtesy of Dr. A. H. Smith, the senior author had the opportunity of studying Dr. Rea's collections of phalloid fungi. Dr. Rea noted the first specimens of *Lysurus mokusin* in Santa Barbara in March, 1941. From that time until the end of his collecting activities he acquired, through his own efforts and those of his neighbors, no less than 130 collections of this species from the Santa Barbara region.

The present paper has grown out of a study of recent collections of clathraceous fungi which appeared in Bermuda grass [*Cynodon dactylon* (L.) Pers.] lawns in Fresno, Yolo, and Sacramento counties, California, particularly after the areas had received an excess of irrigation water. For making available to us the specimens collected in their area, we wish to thank John Bartels, Agricultural Commissioner's Office, Woodland, California, and K. A. Kimble and H. A. McCain, Department of Plant Pathology, University of California at Davis.

The family Clathraceae includes those phalloid fungi (stinkhorns) whose receptacles are stipitate or sessile, clathrate, columnar, or divided into several arms, and whose mucilaginous spore mass is borne on the interior or exterior of the arms or between the arms. In 1931 Cunningham divided the family into three tribes containing eleven genera. The tribe Stellateae, the only one with which we are concerned in California, included the following four genera as keyed out by him:

Arms apically organically united or united by a membrane.

Glebiferous layer composed of irregular pseudoparenchymatous processes

Mycopharus

Glebiferous layer consisting of walls of the chambers of the arms . . . *Anthurus*

Arms apically free, connivent or expanded.

Arms connivent (usually), attached to the apex of a simple cylindrical

(or fluted) stem *Lysurus*

Arms attached laterally to a horizontal discoid expansion of the apex of

the cylindrical stem *Aseroë*

The other seven genera of Clathraceae were placed in the tribes Columnateae and Clathrateae. In a later treatment, Cunningham (1942) placed *Mycopharus* in synonymy with *Lysurus*; the same organization into tribes was retained. Fischer (1933) recognized fifteen genera in the Clathraceae, but he did not arrange them into tribes. He recognized the four genera listed in the key above, as well as *Pseudocolus*, which Cunningham considered to be a synonym of *Anthurus*.

Mycopharus was established by Petch as a segregate from *Lysurus* in which the glebiferous surface of the receptacular arms is formed of a series of minute shingle-like plates in contrast with that of *Lysurus* in which this surface is merely strongly wrinkled longitudinally, possibly as a result of the compact arrangement of the walls of the stipe chambers in this portion of the receptacle. In 1931 Cunningham accepted this basis for differentiation, but in 1942 he reverted to the earlier position that

the two genera were synonymous. In this report Cunningham's 1931 interpretation is being followed and the two genera are considered distinct.

With the exception of some of the Santa Barbara material, which exhibits characters similar in many respects to those of *Mycopharus*, the California specimens studied to date appear to belong in *Lysurus*.

LYSURUS Fr. Syst. Myc. 2: 286. 1822.

Phallus Pers., Syn. Meth. Fung. 245. 1801. *pro min. parte*.

Aseroephallus Lepr. & Mont., Ann. Sci. Nat., Bot. III, 4: 360. 1845.

Anthurus sensu Burt, Mem. Bost. Soc. Nat. Hist. 3: 504. 1894.

Clathraceae; with an egg-like membranous volva; receptacle composed of a glebiferous surface raised on a hollow cylindrical or fluted stipe; stipe white or tinted near the receptacular arms; receptacular arms seated at the top of the stipe, of a more compact tissue, divided into 4-7 arms, arms separate or organically united, grooved on the outside, rounded toward the inside, longitudinally wrinkled, not continuous in the center with the hollow portion of the stipe, covered on the rounded inner glebiferous surface with the ill-smelling gleba.

Type. *Lysurus mokusin* (Cibot ex Pers.) Fr.—only species described in original publication of genus.

KEY TO CALIFORNIA SPECIES OF LYSURUS

Stipe weakly to strongly angular-fluted, upper area red *L. mokusin*
 Stipe cylindrical, upper area brown *L. sulcatus*

LYSURUS MOKUSIN (Cibot ex Pers.) Fries, Syst. Myc. 2:286. 1822. Figs. 1, 2. *Phallus mokusin* Cibot, Nov. Comm. Petrop. 19:373-378, t. 5. 1775. *P. mokusin* Cibot ex Pers., Syn. Meth. Fung. 245. 1801. *Mutinus pentagonus* Bailey, Queensland Bot. Bull. 10:35. 1895. *Lysurus beauvaisii* Möll., Rev. Gen. Bot. 12:61. 1900. *Mutinus pentagonus* var. *hardyi* Bailey, Queensland Agr. Jour. 16:494. 1906. *M. hardyi* Bailey, Comp. Cat. Queensland Pl. 747. 1910. *Lysurus sinensis* Lloyd, Myc. Notes 5: 718. 1917.

Peridium white, 3-6 (-11) cm. long, with white rhizomorphs at base; receptacle 6.5-7.5 cm. long to apex of usually connivent arms; stipe 5 cm. long, 4-7 mm. in diameter, narrow at base and expanding upward, white to orange-pink below, dark orange-pink to reddish above, internally divided into hollow chambers, fluted, the flutings 2-3 mm. deep, continuing above into midribs of receptacular arms; receptacular arms 4-6, 1.5-2 cm. long, red, the texture similar to that of stipe, but wrinkled and more compact, the tips of arms pointed; gleba brownish in color, becoming purplish-black when dry; spores hyaline to pale yellowish, rod-shaped, somewhat rounded at ends, (3.8-) 4.5-5 × (1.2-) 1.5-2.0 μ .

California collections examined.

In Bermuda grass [*Cynodon dactylon* (L.) Pers.] lawn, Fresno, Fresno County, summer, 1952 (DAV). The stipe in this specimen is hollow, 5 cm. long, 4 mm. in diameter at the base and expanding upward, and pen-

tagonal in cross-section, with the surface flutings 1 cm. from tip to tip of the adjoining pairs. The arms are five in number.

In loam in flowerbed at edge of lawn, Bakersfield, Kern County, April 11 and 22, 1936, *Mrs. A. Ashley* and *Mrs. F. Hamlin* (UC 553876). The collectors thought the fungus might have been introduced from Maine with some cultivated plants. When first picked, the stipe in the later collection was orange above, cream below, and the volva was white; a few days later, the stipe had become entirely orange, the arms red, and the glebal mass madder. The odor was described as that of "acetum squill." Too rapid development because of artificial watering caused cracking and abnormalities. Receptacles with both five and six arms are represented in the collection. In more robust specimens, the receptacular arms may be capped by a portion of the volva. The stipes are made up of at least two, possibly three, layers of chambers.

In lawn, Cajon Street, Redlands, San Bernardino County, May, 1944, *G. J. Hollenberg* (UC 695849). When fresh its color was described as pale pinkish. The specimen is evidently immature; the spores measure $3.8 \times 1.2\mu$, and the stipe (the specimen was collected without the peridium) measures 4 cm. in length and 6 mm. in diameter at the top in the dry condition.

The collection of a specimen in Sacramento late in 1956 is represented only by a colored illustration (fig. 1) made by Norma O'Neil of Sacramento. This illustration, which was sent by the Agricultural Extension Office in Sacramento to the University of California at Davis for determination, clearly represents a sporophore of this species. No herbarium specimen is available.

In garden, Santa Barbara, Santa Barbara County, November 18, 1936, *Miss Caroline Hazard* (UC 568835). Upon the arrival of the specimens at Berkeley, Mrs. Vera M. Miller observed that the stipe was not white anywhere, but pinkish throughout, shading down from a color somewhat lighter than that of the arms to an Ibis pink (Maerz and Paul, 1950, Pl. 1, B-10) where the stipe went into the volva, to a very delicate pink at the lower end of the stipe. The stipe is coarsely chambered above, acuminate below, bearing apically the receptacular arms which were united at their tips. One of the receptacles in the collection bears four arms, while the other has six arms. The glebiferous layer is wrinkled and continuous over the unfused area of the arms and the base of the arms above the stipe. The collector reported that when a hot day was followed by a cool night, the texture of the specimens was crisp, while a cool day followed by a cool night resulted in limp receptacles.

In gardens, Santa Barbara, Santa Barbara County, at least 130 collections made between 1941 and 1952 or later by Dr. P. M. Rea or Mrs. Rea or by residents who gave the specimens to Dr. and Mrs. Rea, the collections all deposited at the Herbarium, University of Michigan, Ann Arbor, and dated as follows: March, 1941; June, 1943; April through Novem-

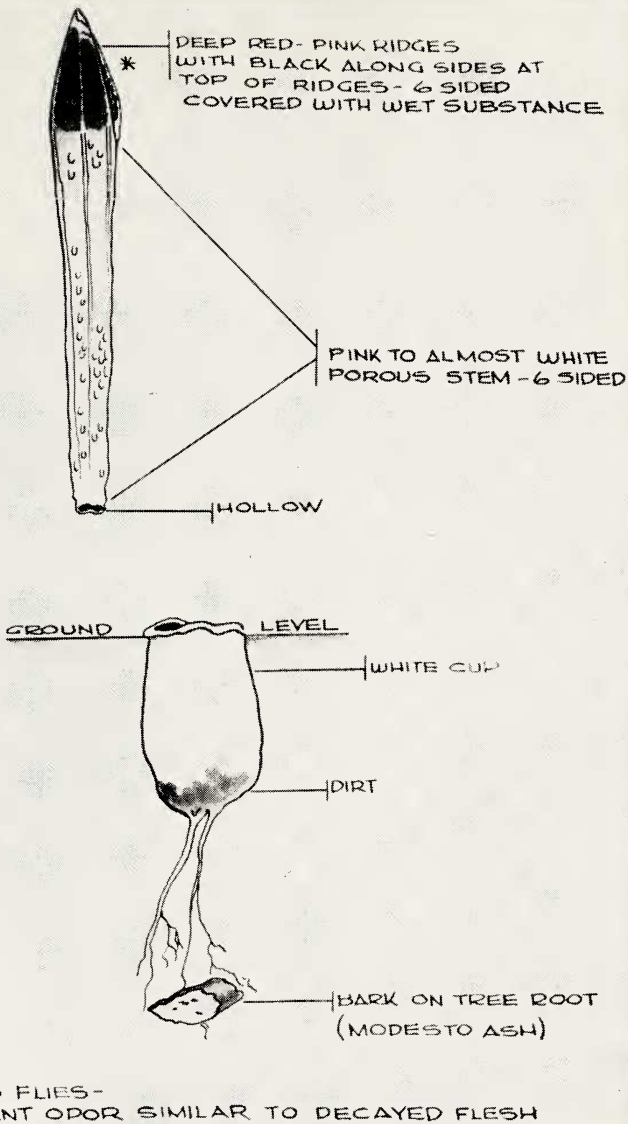


FIG. 1. *Lysurus mokusin* showing habit and mature receptacle. The gleba is shown as occurring between the receptacular arms, not covering their outer surface. Drawing by Norma O'Neil, Sacramento.

ber, 1944; May through September, 1945; May, June, October through December, 1946; January through March, 1947; October, 1952. A wide range of morphological variation is found among these collections as is evidenced in the notes Dr. Rea made from fresh material. On the large

mass of earlier material, he took voluminous notes, among which are three different versions of a paper he was preparing on this species. This material was assembled and developed into a paper for publication by Berta Heidenhain (as co-author) at the University of Michigan (1955). The report gives a complete description of *Lysurus mokusin* throughout its development from the very young buttons or eggs to mature and senescent receptacles.

The senior author has made the following general observations from several representative collections of the above series. Dr. Rea sectioned nine peridia and mounted them on black paper. These sections show that in the unopened receptacle the gleba appears to lie on the outer surface of the receptacular arms and not on the inner surface. The gleba is separated, by plates arising from the center of the backs of the arms, into as many units as there are arms. As was pointed out by Rea and Heidenhain (1955), the glebal masses actually lie between the arms and are attached to their sides, but do not invade the central chamber. The backs, or outer surfaces, of the arms are thus free from glebal material. These surfaces are concave or flat in mature receptacles. However, it has been observed by the present authors that as the arms mature and are raised from the volva, the gleba appears to shift in position and surround the receptacular arms on all surfaces except the backs of the arms.

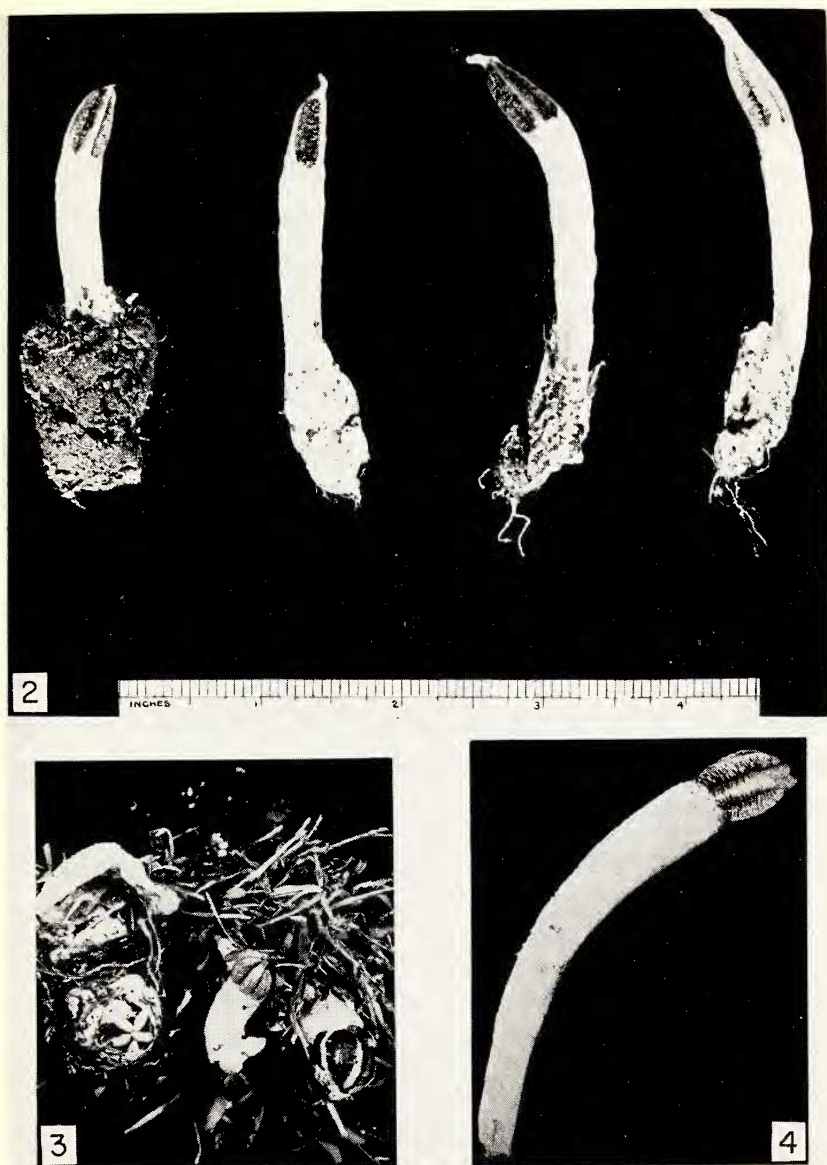
The receptacular arms in the specimens accumulated by Dr. Rea vary from those in specimens in which they are completely free through those which are connivent, those which are held together by fragments or caps of volva material, and those which are organically united by a very small bit of tissue to those which are united in such a way that the receptacular arms form an expanded structure similar to a Chinese lantern and join above the glebiferous surface into an apical spire at least 1.5 cm. long. The longest dry receptacle observed in the Rea collections was 11 cm. long.

Some of the specimens of *Lysurus mokusin* from Santa Barbara, both those of the Reas deposited at the University of Michigan and that of Hazard at the University of California (UC 568835), have characteristics

EXPLANATION OF FIGURES 2-4.

FIGS. 2-4. Development of receptacles in *Lysurus*. FIG. 2. *L. mokusin*. Each of the four fresh specimens shows a different amount of sterile tissue projecting beyond the glebiferous area. Flutings on stipe are apparent and continuous with the outer edge of the receptacular arms between which lies the gleba. Previously unpublished photo by Paul Marshall Rea, Santa Barbara, California. Courtesy of the Herbarium, University of Michigan. FIG. 3. *L. sulcatus*. Cluster of four receptacles in various stages of development. Lower left: young receptacle just breaking through the peridium, the receptacular arms hold the gleba between them; lower right: receptacle with stipe nearly completely elongated, gleba still intact; center: gleba nearly completely removed; upper left: mature receptacle collapsed after removal of gleba. Note cylindrical stipe. Collected at Woodland, and photographed at University of California, Davis, October 1, 1958. FIG. 4. *L. sulcatus*. Single receptacle collected at Woodland, September 23, 1958, showing receptacular arms with wrinkled glebiferous surface.





FIGS. 2-4. Development of receptacles in *Lysurus*.

which in many respects are similar to those of *Mycopharus gardneri* (Berk.) Petch of Ceylon. This latter species was first placed in *Lysurus* by Berkeley, then in *Colus* by Fischer. Petch (1919) established for it the new genus *Pharus*, and later, finding the name *Pharus* to be preoccupied, he (1926) renamed the genus *Mycopharus*, distinguishing it from *Lysurus* on the basis of the type of glebiferous surface on the receptacular arms. He illustrated the genus as having the arms slightly separated from one another below the glebiferous surface. Although, as stated above, some of the characteristics of *Mycopharus gardneri*, the type and at first the only species of this genus, are to be found in some of the Santa Barbara collections of *Lysurus mokusin*, the present authors consider that there are sufficient differences between the two species to justify the separation of the two genera. They differ primarily in the nature of the glebiferous surface, which is composed of tightly packed scales of "pseudoparenchymatous processes" in *Mycopharus* and of tightly packed wrinkles in *Lysurus*; in addition, the stipe is weakly fluted in *Mycopharus* and strongly fluted in *Lysurus*. Among the many specimens of *Lysurus mokusin* from the Rea collection of Santa Barbara, however, there is a wide variety of stipe surfaces, the stipes varying from deeply fluted or winged to shallowly or weakly angular.

LYSURUS SULCATUS (Cooke & Masee) G. H. Cunningham, Proc. Linn. Soc. N. S. W. 56 (3):189, pl. viii, figs. 3, 4. 1931. *L. texensis* Ellis in W. R. Gerard, Bull. Torrey Club 7:30. 1880, *nomen nudum*. *Mutinus sulcatus* Cke. & Mass., Grev. 17:69. 1889. *Lysurus australiensis* Cke. & Mass., Grev. 18:6. 1889. *Anthurus australiensis* (Cke & Mass.) Fisch., Denksch. Schweiz. nat. Gesell. 33:27. 1893. *A. borealis* Burt, Mem. Bost. Soc. Nat. Hist. 3:504. 1894. *Lysurus borealis* (Burt) P. Henn., Hedw. 41:167. 1902. *L. borealis* var. *klitzingii* P. Henn., Hedw. 41:173. 1902. *L. tenuis* Bailey, Comp. Cat. Queensland Pl. 745. 1910. *L. texensis* Ellis (?) in Long, Mycologia 9:271-274. 1917.

Peridium at dehiscence 2-2.3 cm. tall, 2 cm. in diameter at the widest point, rhizomorphic; receptacle 7.5-10.5 cm. long; stipe 6.5-9.0 cm. long, tapering downward, 5-6 mm. in diameter below, 10-13 mm. in diameter at apex just beneath receptacular arms, cream-colored below to yellowish above, composed of one layer of chambers, hollow, apex open, at top of stipe a collar on which are produced 5-7 hollow receptacular arms on the rounded inner surfaces of which is the glebiferous layer; glebiferous layer longitudinally strongly wrinkled, dark olive to blackish; receptacular arms orange-buff to buff to tan in color, composed of very compact tissue with a different appearance from that of stipe, even in length, 6-15 mm. long, 3.5-4 mm. in diameter, tapering to a rather sharp point, more or less flattened on outer grooved surface, the outer surface 1-2 mm. wide, smooth; spores rod-shaped, with rounded ends, slightly yellowish, $3.8-4.3 \times 1.5-1.8\mu$.

In 1880, Gerard noted that Ellis had received a species of *Lysurus* from

Texas which he considered to be new and thus had provisionally named it *L. texensis*. No description was given. In 1917, Long described a *Lysurus* collection from Texas, designating it as *Lysurus texensis* Ellis (?), since this *nomen nudum* had been applied to an undescribed *Lysurus* from Texas. He stated that his material might be only a red form of *Anthurus borealis*. *Lysurus texensis* Ellis in Long is placed in synonymy with *L. sulcatus* because Long's description appears to be based on material of the *L. sulcatus* type rather than of the *L. mokusin* type. In spite of the interpretation by Rea and Heidenhain (1955), Long's description of the stipe is interpreted here as indicating that the walls of the chambers in the stipe wall are polygonal rather than that the stipe itself is polygonal, fluted or winged. Cunningham (1931, 1942) places *L. texensis* in synonymy with *L. sulcatus*, but he lists only Ellis' *nomen nudum* and makes no mention of Long's description.

California collections examined.

In Bermuda grass lawn, Woodland, Yolo County, September 23, 1958, John Bartels; October 1, 1958, K. A. Kimble (DAV). The specimens usually appeared after occasional heavy spray irrigation. They were either solitary in occurrence, grouped in small clusters, or disposed in large numbers in the lawn. In one specimen, the receptacle, instead of bearing six arms of equal length, bore three arms 1.7 cm. long which alternated with three shorter arms, 1.4–1.5 cm. long.

West Sacramento, Yolo County, October, 1958, H. A. McCain (DAV).

In lawn, Fresno, Fresno County, September 16, 1941, George W. Graves (UC 660274). Each of the three somewhat immature receptacles bears six arms. The length of the receptacles in the dried condition is 3 cm., while that of the arms is 5 mm.; the stipe is white, with no indication of the original color, had it been other than white when fresh.

Santa Barbara, Santa Barbara County (P. M. Rea collection, University of Michigan, Ann Arbor). Two small specimens are present in this collection.

In flower garden, "The Flower Shop," San Diego, San Diego County, September, 1913, A. M. Rainford (specimen in alcohol, deposited by Professor W. A. Setchell in the collection of class demonstration material, Botany Department, University of California, Berkeley). According to Dr. Lee Bonar, who reported the existence of this specimen to the senior author (letter, December 11, 1958, the stipe of this specimen is 6.5 cm. long, 2 cm. in diameter at the apex, and 1 cm. in diameter at the base. There are five receptacular arms, which are free at their tips. Of the five arms, one is shorter than the other four; the short arm is 1.7 cm. in length, while the others are 2.1 cm. in length.

SUMMARY

Even though members of the Clathraceae are not commonly found in California, a large number of specimens of *Lysurus* have been found in a

few isolated localities. The two species of *Lysurus* that have been reported from California, *Lysurus mokusin* and *L. sulcatus*, are distinguished primarily on the basis of color and the nature of the surface of the stipe. Since basidia and spores tend to be similar in appearance and size, gross morphological features such as color, the shape of the stipe in cross-section, the type of glebiferous surface, and the extent of the connection of the apices of the receptacular arms serve as the basis for determining the species in the genus *Lysurus*. On the whole, these characters seem to the writers to be of importance only at the species level at our present stage of knowledge of the Phallales. However, the nature of the glebiferous surface of the receptacular arms is considered to be of sufficient importance to separate the two genera, *Lysurus* and *Mycopharus*.

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